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TAXONOMY OF *VERBENA URTICIFOLIA* (VERBENACEAE) AND ITS CLOSE RELATIVES

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ABSTRACT

Verbena urticifolia L., *V. scabra* Vahl, and *V. carolina* L. are distinct species but closely similar among themselves. All three occur natively in the USA, though the latter is primarily a species of Mexico and Central America. *Verbena urticifolia* var. *leiocarpa* is treated here as an intergradient populational variant of *V. urticifolia*. *Verbena carolina* L. is lectotypified here by an illustration in Hortus Elthamensis and epitypified from the Dillenian herbarium—these types were said to be from plants grown from seeds collected in the Carolinas (eastern USA), but their traditional identification as the Mexican species is confirmed here. *Verbena ehrenbergiana* is a closely related species endemic to Mexico and is treated here (including a neotypification) to complete the group. Other type information, descriptions, and a key are provided.

KEY WORDS: *Verbena urticifolia*, *V. scabra*, *V. carolina*, *V. ehrenbergiana*, Verbenaceae

Verbena urticifolia L. and close relatives *V. scabra* Vahl (mainly of the USA) and *V. carolina* L. (mainly of Mexico, but reaching the southwestern USA) have long been recognized as distinct but closely similar species. Aspects of their variability and nomenclature are clarified here in connection with preparation of the FNA treatment of *Verbena*. *Verbena ehrenbergiana* Schauer, restricted to Mexico, is closely related to the three species above and treated here to complete the group.

VERBENA URTICIFOLIA L., Sp. Pl. 1: 20. 1753. **TYPE**: "Habitat in Virginiae, Canadae, *aridis*." **LECTOTYPE** (Méndez Santos & Cafferty 2001, p. 1140): **USA**. Specimen in Linnaean Herbarium, no collection data (LINN 35.13 digital image!). From among several elements of the extant original material for the name, the LINN specimen was chosen as lectotype because it is "the most complete." LINN 35.17 (digital image!), with the notation "Carolina," also appears to be *V. urticifolia* (with subpetiolate leaves).

Verbena diffusa Poir. in Lam., Encycl. 8: 550. 1809. **TYPE**: "Cette plante est cultivee au Jardin des Plantes de Paris; elle croît dans l'Amerique septentionale. (V.s. in herb. Desfont.)." Specimen in Desfontaines Herbarium (holotype: P?). Not listed as such in the fiche catalogue for the Desfontaines Herbarium.

Poiret also described *Verbena diffusa* var. β (also from a specimen in the Desfontaines herbarium), with stems hirsute and spikes erect and scarcely diffuse.

Moldenke (1965a, p. 336) noted that the description of the flowers of *Verbena diffusa* as 'somewhat purple' led him to suspect that *V. diffusa* might be the same entity as *V.* x *engelmannii* Moldenke (= *V. urticifolia* x *V. hastata*).

Verbena incarnata Raf., Atl. J. 154. 1832. *Verbena urticifolia* var. *incarnata* (Raf.) Moldenke, Phytologia 7: 259. 1960. *Verbena urticifolia* forma *incarnata* (Raf.) Moldenke, Phytologia 52: 232. 1982. **TYPE**: USA. Pennsylvania. [Huntingdon, Mifflin, Juniata, or Perry Co.:]: along the Juniata River, *C.S. Rafinesque s.n.* (not located). Moldenke made the transfers to variety and forma without comment.

Verbena urticifolia var. *simplex* Farwell, Pap. Michigan Acad. Sci. 3: 103. 1924. *Verbena urticifolia* forma *simplex* (Farw.) Moldenke, Phytologia 44: 134. 1979. **SYNTYPES: USA**. Michigan. [Oakland Co.]: In woods near Lakeville, 11 Oct 1922, *Billington, Farwell, and Gladewitz 6443* (BLH?, not seen); [Oakland/Wayne Co.]: Northville, *O.A. Farwell 6463* (BLH?, not seen). **LECTOTYPE** (O'Leary et al. 2010): *Farwell 6443* (BLH). Moldenke's transfer of var. *simplex* to the rank of forma was made without comment.

Verbena urticifolia var. *leiocarpa* Perry & Fernald, Rhodora 38: 441, plate 450, figs. 5-8. 1936. **TYPE: USA**. Virginia. Princess Anne Co.: Virginia Beach, rich woods, 10 Sep 1935, *M.L. Fernald, B. Long, and J.M. Fogg Jr. 5013* (holotype: GH digital image!).

Verbena curtisii Moldenke, Phytologia 2: 147. 1946. **TYPE: USA**. North Carolina. "E. Carolina, not date, *M.A. Curtis s.n.* (holotype: GB, herb. G. Geete 5702, LL-photo!). O'Leary et al. (2010) place *V. curtisii* as a synonym of *V. carolina* L.

Plants perennial, fibrous-rooted or sometimes obscurely taprooted. **Stems** erect, 50–150(–250) cm, sparsely to moderately hirsute to hirsutulous or pilose-hirsute, eglandular. **Leaves** ovate to lanceolate-ovate, broadly lanceolate, or oblong-ovate in outline, midstem blades 8–15(–20) cm, margins coarsely serrate to crenate-serrate, hirsutulous or hirtellous to hirsute or strigose-hirsute on both surfaces, eglandular, veins not impressed adaxially; petioles 5–25(–40) mm. **Fruiting spikes** in panicles, elongate and slender with distantly remote fruits, 5–22 cm, bracts; floral bracts ovate-acuminate, 0.5–2 mm, 1/2–2/3 as long as the calyx. **Calyces** 1.5–2.3 mm, strigillose to strigillose-hirsutulous, eglandular, lobes deltate to shallowly deltate-apiculate, incurved by not connivent to subconnivent. **Corollas** white, rarely pinkish, tubes 1.6–2.2 mm, 0.2–0.5 mm longer than the calyx, limbs 1.5–2 mm in diam. **Nutlets** separating at maturity, 1.5–2 mm, commissural faces extending to very tip of nutlets, smooth or rarely with slight development of minutely bullate ornamentation, outer surfaces smooth to shallowly longitudinally ridged, sometimes with cross-ridges distally. $2n = 14$.

Flowering Jun–Oct. Wet woodlands, wet thickets, woods borders, pastures, stream banks, marshy shores, floodplains, shell mounds, ditches, swales, roadsides, fencerows, fields, disturbed sites; ca. 20–1000 m; Man., N.B., Ont., Que., Sask.; Ala., Ark., Conn., Del., D.C., Fla., Ga., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., Nebr., N.H., N.J., N.Y., N.C., Ohio, Okla., Pa., R.I., S.C., S.Dak., Tenn., Tex., Va., Vt., Wisc., W.Va.

Verbena urticifolia var. *leiocarpa* has been recognized as a distinct entity in various floristic treatments (e.g., Fernald 1950; Gleason & Cronquist 1991; Magee & Ahles 1999; Rhoads & Block 2007) but simply as a synonym within *V. urticifolia* by others (e.g., Radford et al. 1970; Wunderlin & Hansen 2008). Cooperrider (1995) found no Ohio plants to identify as var. *leiocarpa*, noting however that "there is a considerable amount of variation within Ohio specimens and some may approach var. *leiocarpa*." Moldenke (1965b) recognized var. *leiocarpa* as distinct and apparently continued to do so, since he later reduced other infraspecific taxa to the rank of forma (see typification and nomenclature above). The PLANTS Database (USDA-NRCS 2010) characterizes the two taxa as broadly sympatric over most of the eastern and central USA.

Contrasts between the typical expression of *Verbena urticifolia* and var. *leiocarpa* and have used terminology as in the summary here, mostly following the initial characterizations in the protologue of var. *leiocarpa*.

1. Leaves strigose to strigose-hirsute on abaxial veins, with hairs up to 1–1.3 mm; flowering branches thicker, usually stiffly ascending, strigose, fruits remote; mature calyx 2–2.3 mm, strigose; floral bracts 1–1.5 mm; nutlets 2 mm, corrugated on the back ..... **Verbena urticifolia** var. **urticifolia**

1. Leaves velutinous to subvelutinous abaxially, with hairs 0.3 mm; flowering branches filiform, loosely ascending or divergent, puberulent, fruits distantly remote; mature calyx 1.7–2 mm, puberulent; floral bracts 0.5–1 mm; nutlets 1.5 mm, plane on the back ..... **Verbena urticifolia** var. **leiocarpa**

In my survey of *Verbena urticifolia*, two extremes of adaxial leaf vestiture can be recognized, corresponding to the illustrations in Fernald (1936), but intergradation between them appears to be complete. Several "nodes" can be recognized in the array of variability: (a) strigose to strigose-hirsute along veins; (b) strigose to strigose-hirsute along veins and lamina; (c) strigose to strigose-hirsute along veins and lamina, with a hirsutulous to hirtellous understory of mostly shorter hairs; and (d) softly hirsutulous to hirtellous on veins and lamina, without the strigose to strigose-hirsute vestiture of longer hairs. Fernald's "velutinous to subvelutinous" corresponds to what is here termed "softly hirsutulous to hirtellous," but they clearly refer to the same state, characterizing var. *leiocarpa*. This variability in vestiture (including the "leiocarpa" variants) is confirmed here to occur essentially throughout the range of the species, from the Atlantic coast westward to Texas and Kansas. I cannot find correlations between any 'node' of the leaf vestiture and any of calyx length or calyx vestiture, spike morphology or spike vestiture, floral bract length, or nutlet size or morphology.

The identity of *Verbena carolina*.

Verbena carolina of Linnaeus in 1759 was based explicitly on an illustration and description by Jacob Dillenius in Hortus Elthamensis in 1732 and identified as "Verbena carolinensis, melissae folio aspero." The protologue referred or alluded to no other plant, except indirectly, through Dillenius's description (see below). Dillenius noted that the plant was grown from seeds collected in the Carolinas ("orta e seminibus Carolinensibus").

The plant illustrated by Dillenius has hirsute stems, subsessile to short-petiolate cauline leaves, and relatively few, compact, and short spikes from distal axils. The spikes apparently are in early development, not lengthened at maturity with widely remote fruits. In addition to the diagnostic "folio aspero" in the Dillenian phrase name, the extended description by Dillenius noted hirsute stems ("caulibus … hirsutis") and leaves rough to the touch ("tactu asperis"). At the end of his description, Dillenius included an entry in John Ray's *Historia plantarum generalis* (H.S. Pet. Raj. Hist. Plant. Tom. III. App. p. 249. num. 10: "10. Verbena *Caroliniana* fol. integro serrato scabro."

Two specimens in the Dillenian Herbarium (images and observations provided by OXF Curator Stephen Harris) are particularly relevant to the consideration here.

Hort-301-388a (Fig. 1) has three plants of the same species. The left plant is labelled by Sherard "carolina ex H. Elth. 1726." The middle plant is labeled (bottom left) in the handwriting of Dillenius: "Verbena Carolin. Melissa folio aspero H. Elth. Verbena Carol. folio integro serrata scabro. Pet. H.S. 10 Raj. Hist. III. App. 249. Eltham 1726" with the number "24." This plant is a very close match for the Dillenius illustration, plausibly even the one used for it (compare Figs. 1 and 2). The right plant is labeled (neither Sherard nor Dillenius) "Verbena carolina Sp. Pl. 29. 12. Feb." (a reference to the entry for *V. carolina* in Species Plantarum ed. 2, 1: 29. 1762, no. 12). Pencilled on the sheet by Asa Gray, above the right label, is "V. polystachya HBK."

Hort-301-388b has a single plant, with two labels in Sherard's handwriting. One label notes "Eltham 1727. … Mexico I think." The other label has "Verbena integrifol. spicis tenuissimis, floribus minimis albus, ~~Mexico~~ (the "Mexico" crossed through).

Despite attestations in the protologue (including the epithet and the illustration) and on the specimens that the plants originated from the Carolinas, both the illustration and associated specimens represent the Mexican species, not *V. urticifolia* or *V. scabra* of the eastern USA.

Seeds from Mexico might have come to Sherard from William Houstoun (1695-1733). According to Clokie (1964), Sherard grew seeds from Houstoun at Eltham, and Houstoun is represented by specimens in the OXF Herbarium. His travels in Mexico (Veracruz and Campeche),

however, apparently were between 1729 and 1733, thus he probably was not the collector of the Dillenian specimens labeled with the years 1726 and 1727. Stephen Harris (pers. comm. Feb 2010) noted that "One can imagine numerous scenarios that might explain Sherard's confusion [about the provenance]. There are other examples in the Sherard Herbarium where Sherard has crossed out localities and changed his mind."

It seems almost certain, though, that Sherard's crossed-out notations of "Mexico" on 301-388b were indeed connected with the real provenance of the plants. Asa Gray's annotation indicates that he identified them as Mexican in origin, and in the Synoptical Flora (Gray 1878), in synonymy of *Verbena polystachya*, he noted "*V. Caroliniensis*, Dill. Elth. ii. 407, t. 301, fig. 388: therefore *V. Carolina*, L. Spec. ed. 2, ii. 29, but not in Carolina," again indicating that he perceived the mismatch between the name (and the intended provenance) and the Sherardian specimens and illustration.

VERBENA CAROLINA L., Syst. Nat. ed. 10, 2: 852. 1759. **LECTOTYPE**: (designated here): [icon] in Dillenius, Hort. Eltham. 2: 407, plate 407, fig. 388. 1732. Fig. 1. Protologue of 1759: "V. tetrandra, spic. filiformibus, fol. indivisis, lanceolatis serratis obtusiusculis subsessilibus. Dill. elth. t. 301. f. 388." In 1762 (Sp. Pl. ed. 2, 1: 29), Linnaeus included a reference to the Petiver specimen in Ray's Historia plantarum. **EPITYPE** (designated here): middle plant of Hort-301-388a, labeled by Dillenius as "Verbena Carolin. Melissa folio aspero H. Elth.," Eltham, 1726 (Dillenian Herbarium, OXF digital image!, Fig. 2).

Verbena caroliniana L. (Syst. Veg. ed. 13, 62. 1774) is an orthographical variant of *Verbena carolina* L. Similarly, Willdenow (Sp. Pl. ed. 4, 1(1): 119. 1797) used the epithet "caroliniana," repeating Linnaeus's original description of *V. carolina* and referring to the Dillenius illustration. Sprengel (Syst. Veg. 2: 748. 1825) also used "caroliniana" as the epithet, citing "Carolina, Mexico. (V. 2serrata Kunth)." *Verbena carolinensis* (Walter) Gmelin ex Small (Fl. S.E. U.S. 1009. 1903), is a synonym of *Verbena carnea* Medik. (Nesom 2010). Michaux (Fl. Bor.-Amer. 2: 14. 1803) attributed the authorship of his *Verbena caroliniana* to Linnaeus, but his description and type specimen refer to *Verbena carnea*.

Verbena polystachya Kunth, Nov. Gen. Sp. (qto.) 2: 274. 1818. *Verbena* [*caroliniana*] var. *polystachya* (Kunth) Loes., Fedde Repert. Sp. Nov. Veg. 9: 687. 1846. **TYPE**: **Mexico**. [Michoacan]. Jorullo, "Crescit in devexis montis ignivomi Xorullo, alt. 600 hex. (Regno Novae Hispaniae)," *A. von Humboldt and A.J.A. Bonpland s.n.* (holotype: P fiche!). Kunth noted "Verbenae urticaefoliae Linn. proxima."

Verbena biserrata Kunth, Nov. Gen. Sp. (qto.) 2: 275. 1818. **TYPE**: **Mexico**. [Edo. Mexico]. "Crescit prope urbem Mexici," *Humboldt and Bonpland s.n.* (P fiche!, photo-MO!). Kunth noted "A Verbenae urticaefoliae vix distinguitur, nisi foliis oblongis serratis, dentibus alternis minoribus."

Verbena veronicifolia Kunth, Nov. Gen. Sp. (qto.) 2: 274. 1818 [non J.E. Smith, Cycl. 36: 28. 1817]. **TYPE**: **Mexico**. [Hidalgo]. "Crescit prope Moran Mexicanorum, alt. 1426 hex," *Humboldt and Bonpland 4065* (holotype: P fiche!).

Verbena hirsuta Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11: 321. 1844. *Verbena carolina* var. *hirsuta* (Mart. & Gal.) Moldenke, Phytologia 44: 473. 1979. *Verbena carolina* forma *hirsuta* (Mart. & Gal.) Moldenke, Phytologia 47: 330. 1981. **SYNTYPES**: **Mexico**. Veracruz. Jalapa, Jun-Oct 1840, *H.G. Galeotti 735* (BR, photo-US, photo-F, photo-NY, K fide Perry 1933); Mirador, *H.G. Galeotti 790* (BR). **LECTOTYPE** (O'Leary et al. 2010): *Galeotti 735* (BR). Moldenke (1963) placed *V. hirsuta* as a synonym of *V. carolina* forma *albiflora* (= *V. menthifolia*).

Verbena mollis Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11: 323. 1844 (non Raf., Atlantic J., 146. 1832). **TYPE**: **Mexico**. Oaxaca. *H.G. Galeotti 737* (holotype: BR). Fide Moldenke (1963a) and from the description. O'Leary et al. (2010) also place it here.

Verbena pauciflora Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11: 324. 1844 [non Turcz. 1863].

TYPE: **Mexico**. Veracruz. Mirador, *H.G. Galeotti 773* (holotype: BR). Fide Moldenke (1963a) and from the description. O'Leary et al. (2010) also place it here.

Plants annual to short-lived perennial herbs, fibrous-rooted. **Stems** 1–5 from the base, erect, 30–100 cm, glabrate to sparsely or moderately hirsute or hirsute-villous, with spreading to upturned, often flattened hairs, eglandular. **Leaves** narrowly elliptic to elliptic-lanceolate or lanceolate, midstem blades 3–8 cm x 8–25(–30) cm, veins not impressed adaxially, margins serrate to serrate-crenate, strigillose to hirsute-strigose adaxially, hirsute to hirsutulous abaxially, eglandular; petioles 3–7 mm. **Fruiting spikes** 5–20 in panicles, elongate and slender with distantly remote fruits, 5–35 cm; floral bracts ovate-triangular to triangular, 0.8–1.2 mm, shorter than the calyces. **Calyces** 1.5–2 mm, hispid-strigose to hirsute-strigose, eglandular, lobes triangular, connivent. **Corollas** lilac to lavender or blue, rarely white, tubes 2.2–2.5 mm, 0.2–0.8 mm longer than the calyces, limbs 1.5–2.5 mm in diam. **Nutlets** adherent until late in ontogeny or weathering, (1.2–)1.5–2 mm, commissural faces extending to very tip of nutlets, smooth, outer surfaces weakly longitudinally ridged, rarely smooth, sometimes with cross-ridges distally. $2n = 14$.

Flowering mostly Aug–Oct. Creek banks, springs, canal banks, canyon bottoms, flood plains, riparian woods, rocky slopes; in the USA at (400–)800–1900 m, in Mexico at (140–)1800–2400(–3000) m; Ariz. (Cochise, Gila, Maricopa, Pima, Santa Cruz cos.); Mexico (Chiapas, Chihuahua, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Edo. México, Michoacan, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Sinaloa, Sonora, Tamaulipas, Veracruz, Zacatecas), Central America (El Salvador, Guatemala, Honduras, Nicaragua).

Verbena carolina is distinct in aspect, compared to *V. urticifolia*, especially because of its smaller, subpetiolate leaves. The species is at the northernmost point of its range in southern Arizona (Cochise, Gila, Maricopa, Pima, and Santa Cruz cos.). A collection from Nevada ([Douglas Co.]: Carson Valley, Aug 1872, *Lemmon 3075*, GH-as cited by Perry 1933) has not been verified here, but this locality is far out of range for the species; at least *V. carolina* has not been subsequently observed in Nevada, and it does not appear to be a member of that state's flora.

The calyces of some plants of *Verbena carolina* are very urticifolia-like, slightly exposing the nutlet apices, but the leaves and fruits are characteristic of the species, e.g., **Nayarit**. 3-4 mi S of Ahuacatlán, 18 Nov 1961, *Gentry et al. 19536* (ARIZ); **Sonora**. El Capitan, 25 Aug 1986, *Martin et al. s.n.* (ARIZ).

The identification by O'Leary et al. (2010) of *Verbena curtisii* Moldenke (here = *V. urticifolia*) as a synonym of *V. carolina* places the latter in the eastern USA; their synonymization of *V. sedula* (a good species) under *V. carolina* places the latter in the Galapagos Islands; their synonymization of *V. litoralis* forma *magnifica* Moldenke (= *V. litoralis*, Nesom 2010x) under *V. carolina* places the latter in Ecuador. I have not evidence that *V. carolina* occurs anywhere except in the range given above.

VERBENA SCABRA Vahl, Eclog. Amer. 2: 2. 1798. **TYPE**: "Habitat in America meridionali," [1786], *Dr. v. Rohr no. 35* (holotype: C, IDC microfiche: Vahl no. 78 I, 5!).

Julius von Rohr in 1786 collected on Martinique, Guadeloupe, Barbados, Antigua, Anguilla, the Virgin Islands, Puerto Rico, and Hispaniola (Howard 1975), and the type of *Verbena scabra* presumably is from the West Indies.

Verbena scabra forma *angustifolia* Moldenke, Phytologia 14: 296. 1967. **TYPE**: **USA**. Texas. Burnet Co.: moist black loam at edge of Beaver Creek, 21 Jul 1966, *J.R. Crutchfield 1837* (holotype: LL! digital image!).

Verbena scabra forma *ternifolia* Moldenke, Phytologia 29: 503. 1975. **TYPE: USA**. Texas. Burnet Co.: Dove Creek on the Tweedy Ranch at Knickerbocker, creek riparian, 19 Jul 1974, *R. Eckhardt 1739* (holotype: LL! digital image!).

Plants annual to short-lived perennial herbs, fibrous-rooted, sometimes appearing rhizomatous. **Stems** usually 1 from the base, erect, (50–)70–170 cm, moderately to densely hispidulous to hispid-hirsute, hirsute, or hirsute-strigose, eglandular **Leaves** ovate-lanceolate to ovate-elliptic or lanceolate, midstem blades (3–)5–12 cm x 15–60 mm, margins evenly serrate, scabrous or hispidulous to hispid or hispid-hirsute adaxially, hispid to hirsute-strigose abaxially, eglandular, veins not impressed adaxially; petioles 5–15(–30) mm, narrowly winged or nearly indistinct. **Fruiting spikes** 3–7(–15) in panicles, elongate and slender with distantly remote fruits, 5–40 cm; floral bracts ovate-lanceolate to triangular or narrowly triangular, 1–1.5 mm, shorter than the calyces. **Calyces** 1.5–2.5 mm, hispidulous to hispid-strigose or hirtellous with upturned hairs, eglandular, lobes lanceolate to triangular, connivent. **Corollas** pinkish to bluish, lavender, or purple, tubes 1.5–1.7 mm, 0.2–0.5 mm longer than the calyces, limbs 1.4–2.2 mm in diam. **Nutlets** separating at maturity, 1–1.5 mm, commissural faces extending to very tip of nutlets, consistently silvery white densely papillate-bullate, outer surfaces deeply ridged and grooved, often with prominent cross-ridges. $2n$ = unknown.

Flowering (Apr–)Jun–Sep. Low woods, open slash pine woods, marshy shores, wet thickets, floodplains, stream banks, shell mounds, back dunes and flats, swales, ditches, sandy fields, disturbed sites; 10–100 m; in the western USA—canyons, marshes, river and pond edges, 300–2100 m; Ala., Ariz., Calif., Fla., Ga., La., Md., Miss., N.Mex., N.C., S.C. Tex., Va., W.Va.; Mexico (Baja California, Chihuahua, Coahuila, Sonora), Bermuda, Bahamas, West Indies (Cuba, Hispaniola, Jamaica, Puerto Rico).

Verbena scabra in the USA mostly occurs in marshy habitats near the Atlantic and Gulf coasts. In inland localities and its range across Texas westward to California (apparently adventive?), it usually grows in wet places. The species was attributed to Arkansas by Moldenke (1964; Drew Co.: *Demaree 13696*, SMU!; *Demaree 24748*, BM, SMU!), but these are identified here as *V. urticifolia*. Similar observations by Smith (1988) and Brent Baker (pers. comm. 2010)—Arkansas plants previously identified as *V. scabra* actually are *V. urticifolia*—preceded mine. The other Arkansas collection cited by Moldenke, however, is indeed *V. scabra*: Washington Co.: Fayetteville, 29 Jul 1927, collector not specified but handwriting on an original ("Herbarium of the University of Texas" label is possibly that of B.C. Tharp? (TEX). Given the dubious circumstances of the label and lack of other evidence that *V. scabra* occurs in the state, it is not considered here to be a member of the Arkansas flora.

Verbena scabra usually is distinct from *V. urticifolia* in scabrous or hispidulous to hispid leaf vestiture, but plants of *V. scabra* sometimes (rarely) develop slightly longer hairs and the vestiture becomes nearly hirsute, approaching *V. urticifolia*. More commonly, leaves of *V. urticifolia* may develop near-hispid vestiture approaching that of *V. scabra*. In such cases, other features can be used to distinguish them, as in the key below. The differences in calyx morphology and petiole elaboration are the most consistent. I have not seen an unequivocal intermediate between the two species, but given the ease with which vervains hybridize and the probable difficulty in detecting a hybrid between these two, it's not unlikely that they are formed.

Verbena scabra has sometimes been described as rhizomatous (e.g., Radford et al. 1970; *Wright & Baker 1683*, ASU, from Pinal Co., Arizona). The plants most commonly are collected as shallowly fibrous-rooted annuals or short-lived perennial, occasionally developing a taproot, but the basal portions of the stems sometimes apparently are procumbent and rhizome-like, layering and producing adventitious roots. I have seen examples of such from Alabama, California, Florida, Louisiana, Mississippi, and South Carolina, and from Hispaniola. One collection from Baja

California (Santo Tomás, 15 Jul 1885, *Orcutt 1302*, MO) bears a plant with fibrous roots, clearly annual in duration; the plant of a duplicate sheet (MO) has a layered, "rhizomatous" portion 12 cm long. Other collections are unequivocally rhizomatous (vs. procumbent and layering): **Bahamas**. Eleuthera, 16 Aug 1977, *Correll 48999* (MO). **USA**. **Arizona**, Gila Co., 20 mi N of Rice, 4 Oct 1927, Harrison 4897 (ARIZ); Yavapai Co., Page Spring State Fish Hatchery, along edge of stream, 17 Aug 1966, *Crutchfield 1966* (LL); **California**, Los Angeles Co., Verdugo Canyon, 11 Aug 1910, *Blake 676* (LL); **New Mexico**, Eddy Co., seeping area near Rattlesnake Spring, 9 mi SW of White City, 26 Oct 1966, *Crutchfield 2407* (LL); **Virginia**, Isle of Wight Co., 27-29 1940, *Fernald & Long 12785* (TEX). **Mexico**. **Coahuila**, 1.5 mi W of Ocampo at "Parque La Mota," along stream, 1150 m, 25 Sep 1998, *Henrickson 20511* (TEX); Sierra de San Antonio, canyon San Antonio de los Alamos, moist ground in shaded canyon, 2-3 Sep 1940, *Johnston & Muller 877* (TEX). Some collections are of plants with leaf-tipped basal "offsets" (Jamaica, Dec 1890, *Hitchcock s.n.*, MO, offsets 12 cm long; Jamaica, 9 Jun 1963, *Proctor 23622* (LL), offsets 3 cm long; California, 19 Aug 1910, *Blake 788* (LL), offsets 8 cm long; Virginia, 20 Oct 1936, *Fernald & Long 6863*, MO, offsets 4–5 cm long).

VERBENA EHRENBERGIANA S. Schauer, Linnaea 20: 477. 1847. **SYNTYPES**: **México**. Protologue: "In Mexico, pr. los Reyes, C. Ehrenberg 517 et 713." [Edo. México]. Barranca prope los Reyes, [probably 1832, fide Urban 1897], *C. Ehrenberg 713* (B-s.n. photo-MO!, plant on right; B-17414 photo-F!, photo-MO!, photo-TEX!). Moldenke (1963b) noted that *713* is the type but did not mention that is it one of two syntypes. The B specimens are no longer extant, thus a widely distributed **NEOTYPE** is designated here: **Mexico**. Moist places near Monterrey, Jul 1888, *C.G. Pringle 1948* (MO!; isoneotypes: BR, F, GH, MEXU, MICH, NY, PH, S, UC, US, VT). Duplicates as cited by Perry (1933) and Moldenke (1963b). A neotype to be designated by O'Leary et al. (2010), said to be an Ehrenberg collection (P: "*C. Ehrenberg 153*," from Wartenberg in Veracruz) was instead collected by Louis C. Ervendberg, who collected plants in that region for Asa Gray from early 1857 to late 1860.

Verbena ehrenbergii var. *richardsonii* Moldenke, Phytologia 38: 499. 1978. **TYPE**: **México**. Tamaulipas. Gómez Farias area, Rancho del Cielo, bird census area, near ranch, 29 May 1969, *A. Richardson 1234* (holotype: LL! digital image!; isotype: LL! digital image!). O'Leary et al. (2010) place var. *richardsonii* as a synonym of *V. carolina* L.

Plants perennial herbs, taprooted or fibrous-rooted, sometimes appearing rhizomatous. **Stems** mostly 1 from the base, erect, 50–100 cm, hirsute, hirsute-pilose, or most often bristly-pilose, eglandular. **Leaves** ovate to narrowly ovate or lanceolate to oblong-lanceolate, basal not persistent, midstem cauline 2–7 cm x (8–)10–30 mm, margins coarsely serrate to crenate-serrate, usually with a distinct pair of narrow lobes near the base, sparsely hirsute to strigose-hirsute or strigose adaxially, hirsute abaxially mostly along the veins, eglandular, usually with a petiole or petiolar region 5–15 mm. **Spikes** (3–)5–25(–40) from distal branches, elongate and slender with distantly remote fruits, 4–18 cm; floral bracts ovate-lanceolate, 1–1.5 mm, shorter than the calyces. **Calyces** 1.5–2.1 mm, hirsute-strigose to loosely strigose, eglandular, lobes subulate, incurved. **Corollas** white (pale lilace or blue in Querétaro), tubes 1.7–2 mm, 0.1–0.5 mm longer than the calyx, limbs 1–2 mm in diam. **Nutlets** 1–1.5 mm, separating tardily, commissural faces reaching the tip, bare. $2n = 14$.

Flowering (Apr–)May–Aug(–Oct). Road banks, river beds, moist places, rocky hills, thorn scrub, cloud forest; (40–)100–2000 m. Mexico (Coahuila, Hidalgo, Nuevo León, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Veracruz).

Verbena ehrenbergiana has been attributed to Arizona based on a specimen at TEX collected in "Arizona" without definite locality (Kearney & Peebles 1961; *Stalmach 198*, TEX, as cited by Moldenke 1963b), but this locality is far out of range for the species. It has never been otherwise reported from the USA and is not considered here to be a member of the Arizona flora.

Verbena ehrenbergiana is distinct among its closest relatives in its consistently 3-lobed leaves and bristly stem vestiture. The calyx lobes are deltate-triangular and slightly connivent but not as long as those of *V. scabra*. It apparently is restricted to northeastern Mexico—I have not seen collections cited by Moldenke (1963b) from Distrito Federal ("*Arsene 8829* in part," B) and Michoacan ("*Arsene 8829* in part," NY), but the species has not otherwise been reported from that area. It was not included in the treatment for the Valley of Mexico (Peralta 1985).

The types of *Verbena ehrenbergiana* var. *richardsonii* have coarsely toothed leaves without the typical pair of basal lobes, but in other features (the deltate calyx lobe and bristly-pilose stems) they clearly belong with *V. ehrenbergiana*. Collections from the Rancho del Cielo area are the only ones observed over the range of the species without the basal lobes, but the Rancho del Cielo plants are variable in basal lobing—some others also are unlobed (*Richardson 216*, *293*, and *Sullivan 554*), while the rest are typically lobed.

Additional specimens examined and cited (herbaria without exclamation points are from Perry (1933), Moldenke (1963b), and Nash and Nee (1984)). **Coahuila**. El Bajío, Buenavista, Saltillo, area cercanes al arroyo y cultivos, 1850 m, 12 Oct 1980, *Carranza & Villarreal 1401* (ARIZ!). **Hidalgo**. Along Hwy 85 between Tamazunchale and Jacala, 37 mi SW of Tamazunchale near Palomas, cloud forest on steep roadbanks, 1500 m, 25 Jun 1977, *Croat 39305* (MO!) and *Croat 39343* (MO!); Jacala, 12 Aug 1937, *Edwards 757* (MO!, TEX!); Jacala, 4800 ft, 12 Aug 1937, *Fisher 46169* (MO!, US); 12 mi up mine road W of Mex 85, 2 mi N of Posada de Rey, Zimapan, 5 Jul 1966, *Mears 299a* (TEX!). **Nuevo León**. 21.2 mi N of Montemorelos, out of Margarita, Hwy 85 between Monterrey and Montemorelos, thorn scrub community, 9 Aug 1972, *Dziekanowski et al. 1712* (MO!); Mpio. Iturbide, below San Pedro Iturbide, IRF Iturbide, 1070 m, 25 Sep 1979, *Hinton 17609* (TEX!); Mpio. Iturbide, Iturbide –>Camarones, oak and pine woods, 1580 m, 9 Jun 1991, *Hinton 21398* (TEX!); Mpio. Aramberri, Cerro El Viejo, pine forest, 1255 m, 2 Oct 1993, *Hinton 23827* (TEX!); Monterrey, 21 Jul 1933, *Mueller 156* (TEX!); wooded waterway below Alamar, ca. 15 mi SW of Galeana, dense woods, 21 Jun 1934, *Mueller 1132* (TEX!); Mpio. Zaragoza, ca. 3-7 mi ESE of Zaragoza, SW side of Cerro Viejo peak, oak-pine woods, 2000 m, 22 Sep 1993, *Nesom 7725* (TEX!); Mpio. Galeana, Hacienda Pablillo, 26 Aug 1936, *Taylor 238* (MO!, TEX!). **Puebla**. Pahuatlan, 12 Jul 1913, *Salazar s.n.* (MEXU, US). **Queretaro**. Mpio. Pinal de Amoles, Ahuacatlán, 1400 m, 24 Dec 1982, *Hernandez M. 9287* (TEX!); Pinal de Amoles, bosque de *Pinus patula*, 2600 m, 10 Mar 1978, *Zamudio 2675* (TEX!). **San Luis Potosí**. Mpio. San Antonio, Between Tanjasnec and San Pedro, 26 Oct 1978, *Alcorn 2066* (TEX!). **Tamaulipas**. Mpio. de Gomez Farías, region of Sierra de Guatemala, at and slightly above Aguacates junction, ca. 5 km WNW of Gomez Farías, ca. 600 m, 19-25 Aug 1984, *Johnston 12801* (TEX!); Victoria, 16 Oct 1937, *Kenoyer s.n.* (MO!); Mpio. de Gomez Farías: Rancho del Cielo: between red gate and ranch, 20 Jun 1968, *Richardson 188* (LL); between gate and ranch, 20 Jun 1968, *Richardson 216* (LL); Cathedral Cave, near ranch, 24 Jun 1968, *Richardson 293* (LL); road near ranch, 28 Dec 1968, *Richardson 1116* (LL); 27 km SE of Miquihuana on road to Palmillas, broad damp river bed, 2025 m, 13 Aug 1941, *Stanford et al. 891* (ARIZ!, MO!, DS, NY, WTU); Mpio. de Gomez Farías: Sierra de Guatemala, San Pablo, and just below San Pablo on road toward Gomez Farías, 3500 ft, oak-sweetgum, 10 Jun 1971, *Sullivan 409* (TEX!); W of San Pablo toward Indian Springs, 3500 ft, 16 Jun 1971, *Sullivan 475* (TEX!); Sierra de Guatemala, between Old Company Clearing (4000 ft) and the Malacati turnoff (4200 ft) on road between Rancho del Cielo and Julilo, humid oak-sweetgum forest on limestone, 22 Jun 1971, *Sullivan 554* (TEX!). **San Luis Potosí**. Río Verde, 17 Nov 1910, *Orcutt 5423* (MO!); Minas de San Rafael, Bagre, Jul 1911, *Purpus 5451* (F, GH, MO!, NY, US). **Veracruz**. No collection data [near Tantoyuca], *Ervendberg 153* (GH); Misantla, Santa Cruz de Hidalgo, carretera Misantla-Martinez de la Torre, selva mediana subperennifolia, secundaria, zona cafetalera, 140 m, 26 Apr 1976, *Hernandez et al. 154* (F, MEXU, MO!, NY, XAL).

Key to the species of the *Verbena urticifolia* group

1. Leaves 3-lobed ..... **Verbena ehrenbergiana**
1. Leaves not lobed.

2. Leaves mostly sessile to subpetiolate; adaxial leaf surfaces strigillose to hirsute-strigose; calyx tapering distally to lanceolate to triangular lobes, connivent; corollas lilac to lavender, rarely white, tubes 2.2–2.5 mm ..... **Verbena carolina**
2. Leaves mostly petiolate; adaxial leaf surfaces either densely scabrous or sparsely pilose to glabrous to glabrate; calyx lobes lanceolate to triangular and connivent or deltate and not connivent; corollas either mostly white or blue to purple, tubes 1.5–2.2 mm.

3. Adaxial leaf surfaces hirsutulous to hirsute or strigose-hirsute; calyx abruptly narrowed distally to deltate to shallowly deltate-apiculate lobes, incurved but not connivent or subconnivent, top of the nutlets exposed; corollas white, rarely pinkish; nutlet outer surfaces smooth to longitudinally ridged, sometimes with cross-ridges distally, commissural faces smooth or rarely with slight development of minutely bullate ornamentation ..... **Verbena urticifolia**
3. Adaxial leaf surfaces densely scabrous or hispidulous to hispid or hispid-hirsute; calyx tapering distally to lanceolate to triangular lobes, connivent, top of nutlets obscured; corollas mostly pinkish to bluish, lavender, or purple; nutlet outer surfaces deeply ridged and longitudinally grooved, often with prominent cross-ridges, commissural faces consistently densely silver-white minutely papillate-bullate ..... **Verbena scabra**

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Figure 1. Illustration by Dillenius in Hortus Elthamensis of "Verbena carolinensis Melissae folio aspero," the lectotype of *Verbena carolina* L. See comments in text.

Figure 2. Specimen from the Dillenian Herbarium (OXF), Hort-301-388a. The middle plant is the epitype for *Verbena carolina* L. See comments in text.